OBSERVATIONS ON THE IMMATURE STAGES OF *PROTODICTYA HONDURANA* (DIPTERA: SCIOMYZIDAE)[1]

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Although the reference literature is confused concerning the food habits of sciomyzid larvae (cf. Sack, 1938; Bertrand, 1954; and others), studies initiated several years ago by Berg seem to warrant the conclusion that larvae of this family feed exclusively on the soft parts of gastropod mollusks. Berg (1953) reported the feeding activities of larvae of six species and suggested that the family may be "integrated biologically by the common food preferences of their larvae." Subsequent investigations have not only supported this hypothesis, but have disclosed interesting differences in the associations of various larvae with their snail prey.

Larvae belonging to the genera *Sepedon* and *Dictya* characterize the aquatic, predatory Tetanocerinae, which kill their prey quickly, operate with efficiency in water as well as on land, and commonly kill more than a dozen snails during the growth of each larva (Berg, *et al.,* 1955). At the other extreme, terrestrial, parasitoid larvae of some Sciomyzinae may feed on a snail for 7 or 8 days before killing it and confine all of their feeding to the one snail (Foote, 1959). Other species have intermediate and less fixed habits. The larvae of *Atrichomelina pubera,* for instance, resort to predatory, parasitoid, or even saprophagous feeding, depending on the food available and on the intensity of intraspecific competition (Foote, *et al.,* 1960).

Most of the publications on Sciomyzidae that present detailed biological notes and diagnostic figures and descriptions of immature stages concern species of Sciomyzinae. *Protodictya hondurana* Steyskal is a member of the Tetanocerinae, and the immature stages obtained in laboratory rearings present morphological and behavioral differences from those of the Sciomyzinae. Since both the larvae and the puparia of this species have evident aquatic adaptations, it might be expected to display larval feeding habits

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essentially the same as those of *Dictya* and *Sepedon*. However, *P. hondurana* differs from these typical aquatic predators in this and in other respects.

The genus *Protodictya* was erected by Malloch (1933) and was based upon specimens from several localities in Chile. It can be distinguished from other members of the Tetanocerinae by the combination of a white, densely pubescent arista, a triangular third antennal segment, and a black spot in the middle of the face, as in *Dictya*. Steyskal (1950) enumerated 6 species referable to this Neotropical genus from Mexico and from Central and South America. He described *P. hondurana* in this paper, based upon three specimens collected at Pt. Cortes, Honduras; St. Engracia, Tamaulipas, Mexico; and Granada, Nicaragua. These three locality records appear to be the only ones published for this species, but two more are added in the present paper.

With their long, porrect antennae and frog-like posture, *Protodictya* adults bear so much resemblance to those of *Sepedon* that two species now included in the genus were originally described in *Sepedon* (Schiner, 1868, van der Wulp, 1897). However, all species of *Protodictya* differ from *Sepedon* in bearing the prominent, median, black spot on the face, four scutellar bristles, and dark, metallic spots at the bases of the thoracic hairs.

Laboratory rearings of *P. hondurana* were initiated with feral adults collected 2.1 kilometers east of Barberena, Santa Rosa, Guatemala (elevation 1341 meters), and 9.2 kilometers east of San Lorenzo, Valle, Honduras (elevation 60 meters). These collections were made on July 22 and July 30, 1958, respectively. Both of the collection sites were open, wet meadows that were in use as pasture. Adults were captured by sweeping the various grasses and sedges in the moist depressions of these areas. They were transported to the laboratory at Ithaca, New York, for observation and rearing of the immature stages.

Eight-ounce, wide-mouth, glass jars in which the flies were confined for mating and oviposition were prepared in advance to supply certain physiological requirements. The bottom of each jar was covered with a layer of living moss about one-half inch deep. Moistened every day, this moss provided water for drinking and maintained high humidities comparable with those in natural habitats. One or two sections of *Typha* leaf standing almost vertically on the moss provided natural resting surfaces and sites for oviposition. A small pellet of food, a mixture of brewers' yeast and honey with a pinch of calcium proprionate added to inhibit mold, was pressed against the inside shoulder of each jar. (No

attempt was made to provide a carefully balanced, chemically defined diet, and the proportions used were determined solely by the criterion of proper consistency. It had to be sticky enough to adhere to the glass, yet dry enough to remain in place for days without liquefying and running down into the moss.) Two or three living snails of different species were placed on the moss, because the presence of snails may stimulate ovipostion. After the flies were admitted, each jar was covered by a piece of double-thickness cheesecloth, secured in place by one or two rubber bands.

Adults maintained in these breeding jars mated readily, assuming mating postures similar to those of certain other species of Sciomyzidae. The male stood over the female and grasped her antennae with his fore tarsal claws. His middle legs were extended laterally. His body, and his flexed hind legs resting on the female's abdomen, held her wings spread.

Female flies laid numerous eggs on the sides of jars and on the *Typha* leaves. They were usually arranged in vertical rows, lying end to end rather than side by side as in most species of *Dictya* and *Sepedon*. The eggs were transferred to one-ounce, wide-mouth, stoppered, glass jars, supplied with a layer of moist sand ⅛ to¼ inch deep, for hatching and rearing of the larvae. With the laboratory temperature varying between 20 and 28 degrees Centigrade, hatching occurred in 3½ to 5 days.

The newly hatched larvae attacked and killed small individuals (2–6 mm. in diameter) of *Helisoma trivolvis* (Say) and *Biomphalaria* (= *Australorbis*) *glabratus* (Say). Their attacks were swift, and the snails bled profusely soon after the larvae entered their shells. Except for the forthright, decisive attacks, however, their feeding behavior is very different from that of other aquatic tetanocerine larvae which resemble them morphologically. After feeding to repletion, larvae of *P. hondurana* remained within the shells of the snails they had killed until they again became hungry, when they fed again on the same snails. They seemed reluctant to leave the shells even when the snail tissues reached advanced stages of decay. In fact, they usually did not leave until all of the malodorous, liquefied material was consumed.

In their tendency to remain within snail shells even when not feeding, their tolerance of putrescent conditions, and their willingness to feed on decayed snails, these larvae differ from all other known tetanocerine larvae and especially from the aquatic species in closely related genera. The known larvae of *Sepedon* and *Dictya,* for instance, leave their victims as soon as their immediate hunger is satisfied, show considerably more inclination to kill new

snails than to return to any that have been dead for several hours, and even die (in closed rearing jars) if the dead snails are not removed every day. The more parasitoid, terrestrial, first instar larvae of certain species of *Tetanocera* and *Hoplodictya* rest within shells of their hosts between feedings, but they feed in such a way that the snails remain alive until after the first larval molt. When the snails finally die, these larvae are somewhat tolerant of putrescent conditions, but not nearly as tolerant as *P. hondurana* larvae. Among the Sciomyzinae, where parasitoid feeding commonly changes to saprophagous feeding after death of the host snail, feeding behavior similar to that of *P. hondurana* is found especially in the larvae of *Atrichomelina pubera* (Foote, *et al.*, 1960).

Tolerance of putrescent food and the habit of remaining in shells that contain it may be primitive conditions, as was suggested concerning *A. pubera* (Berg, *et al.*, 1959). Alternatively, this way of life may result from secondary specializations, two possible advantages of which are apparent. A tolerance for putrescent food, enabling larvae of this species to utilize each snail more completely, would have survival value if the food supply ever is limited. If the breeding sites are often dried completely by sun and wind, the habit of remaining for days in the moisture within a snail shell may be instrumental in avoiding death from desiccation.

Laboratory observations made on these larvae suggest that their float hairs and other "aquatic" adaptations may not be used primarily to fit them for life in aquatic habitats at all. Although this clearly is the principal use of similar adaptations in larvae of *Sepedon, Dictya,* and most other tetanocerine genera, larvae of *P. hondurana* apparently use them primarily to avoid complete immersion and asphyxiation in decayed and liquefied snail tissues. In other dipterous families, many larvae that do not live in aquatic habitats have float hairs, and the explanation commonly accepted for this phenomenon is that they must remain afloat in the liquid substance that functions both as their food and as the medium in which they live.

If the first snails killed by newly hatched larvae were relatively large (7–10 mm. in diameter), the larvae usually remained in these shells until after their first molt. Some of the cast exuviae were found in the shells, and second instar larvae were observed continuing their feeding activity. Because many exuviae were immersed in liquefied snail flesh and could not be found, it was often difficult to determine the duration of larval stadia.

As with most cyclorrhaphous Diptera, three larval instars and three stadia were observed. Durations of larval stadia were ascer-

tained in eight instances and were as follows: first, 2–5 days; second, 3–6 days; third, 9–13 days. Duration of the larval stadia seemed to be influenced by the size of snails offered the larvae. If a third instar larva was given a fairly large (10–14 mm. diameter) *H. trivolvis,* the larva obtained sufficient food to complete its development and matured directly and rapidly. But if the food snail was smaller, the larva presumably remained in the empty shell 4 or 5 days after consuming all edible material, apparently not feeding and developing more slowly. Multiple infestations in the rearing jars also apparently deprived larvae of sufficient food and prolonged their stadia.

Mature larvae left their snails and crawled about in the jar for twenty-four to thirty-six hours before burrowing into the sand and forming puparia. Pupation time in the laboratory was 10–12 days.

The time elapsed between emergence of five laboratory-reared female flies and appearance of their first eggs ranged from 6 to 14 days, averaging 9.2 days. Two females were observed mating 36–48 hours after they emerged.

The nutrition flies receive after reaching the adult stage apparently is very important in determining the number of eggs laid. Two females laid 141 and 151 eggs in the two weeks after their first eggs were laid. In the two weeks following, their egg laying declined to 57 and 43 eggs, respectively. Because the honey-yeast food mixture may not have been supplying all the nutrients neces-

Explanation of Plate

Fig. 1, Posterior spiracular disc, third instar larva; DL—dorsal lobe, DIL—dorsolateral lobe, FH—float hair, LL—lateral lobe, SS—spiracular slit, ST—stigmatic tube, StS—stigmatic scar, VL—ventral lobe, VlL—ventrolateral lobe. Fig. 2, Same, second instar larva. Fig. 3, Same, first instar larva. Fig. 4, Anterior spiracle, third instar larva. Fig. 5, Cephalopharyngeal skeleton, first instar larva. Fig. 6, Same, second instar larva. Fig. 7, Cephalopharyngeal skeleton, third instar larva; AT—accessory teeth, DC—dorsal cornua, ES—epistomal sclerite, HS—hypostomal sclerite, LS—ligulate sclerite, MH—mouthhook, PS—pharyngeal sclerite, SDA—salivary duct aperture, VA—ventral arch, VC—ventral cornua. Fig. 8, Puparium, dorsal view. Fig. 9, Accessory teeth, mouthhook of third instar larva. Fig. 10, Ventral arch, third instar larva, ventral view with anterior margin on left. Fig. 11, Puparium, lateral view. Fig. 12, Egg, dorsal view, micropylar end to the right.

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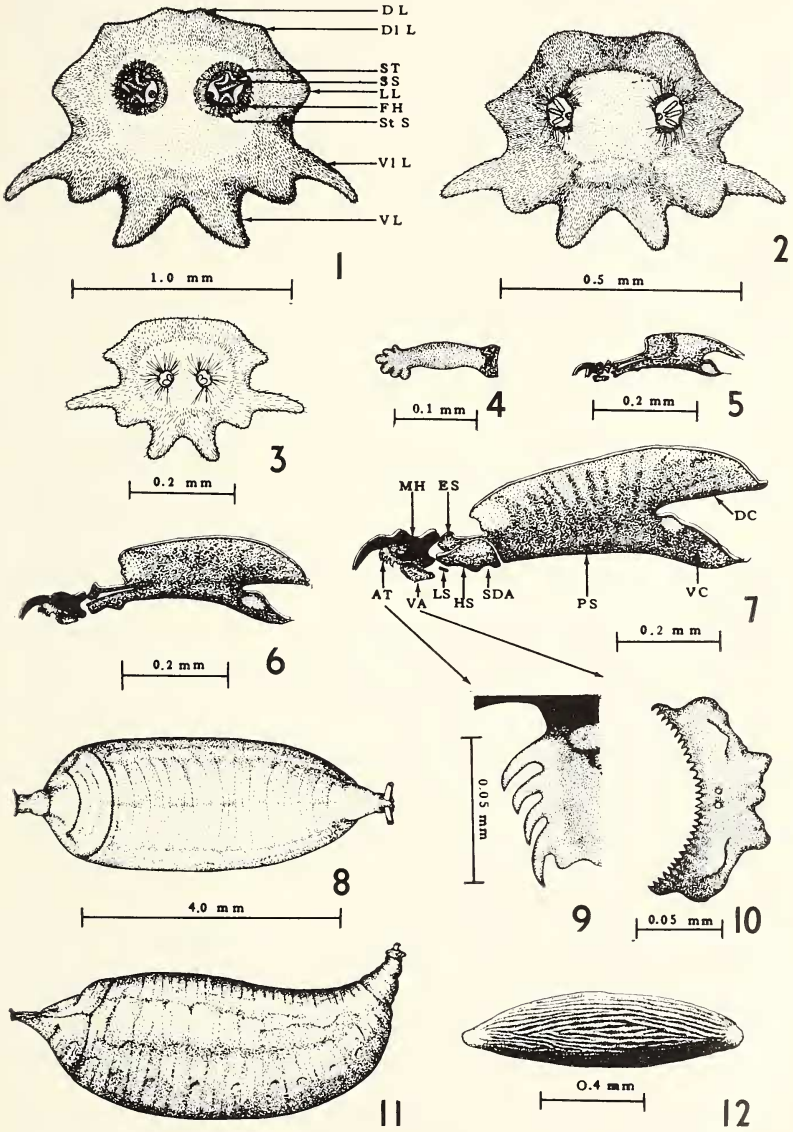

sary for full egg production, crushed snails were added to the breeding jars as suggested by Chock (personal communication). During the following ten days, these flies laid 119 and 126 eggs, respectively.

The complete life cycle ranged from 33½ to 55 days in the laboratory. This suggests that under continuously favorable conditions *P. hondurana* could produce six to ten generations per year. A female fly oviposits over a long period of time (the period apparently being determined by adult nutrition), and one may still be laying viable eggs after her oldest daughters have started to oviposit. Thus the generations would be expected to spread in time and to overlap each other, becoming unrecognizable in nature.

First-generation adults lived from 32 to 177 days under laboratory conditions (32–177 for five females, 62–157 for eight males).

Description of Immature Stages

Egg: (Fig. 12). White. Length 1.08–1.13 mm. ($\bar{x}$ = 1.10 mm.); width 0.30–0.36 mm. ($\bar{x}$ = 0.32 mm.). Twelve to sixteen low, longitudinal ridges visible dorsally; crest of each ridge undulating, giving ridge appearance of being interrupted; ridges anastomosing at each end of egg. Ventral and lateral surfaces with low, longitudinal ridges, as dorsal surface. Micropyle at wide, bluntly rounded end of egg, shielded dorsally by single, rounded tubercle covered by minute punctations. End opposite micropyle terminating in narrower, hemispherical to conical tubercle also bearing minute punctations. (Based on 13 specimens.)

First instar larva: White, integument transparent. Length 1.5–3.9 mm. ($\bar{x}$ = 2.4 mm.); width 0.2–0.7 mm. ($\bar{x}$ = 0.37 mm.). Resembling third instar larva in general body shape and distribution of hair patches and body tubercles. Sensory papillae and plates on segment 1 as in third instar. No anterior spiracles. Cephalopharyngeal skeleton (Fig. 5), length 0.26–0.33 mm. ($\bar{x}$ = 0.30 mm.); with paired mouthhooks, each mouthhook bifid anteriorly, articulating with ventral arch below and fused hypostomal-pharyngeal sclerite behind. Posterior spiracular disc (Fig. 3) with 3 pairs of prominent lobes; ventral pair only slightly longer than wide, rounded apically; ventro-lateral pair with broad basal portion, elongate apical portion more than twice as long as wide arising dorsally; lateral lobes evident as short, conical protuberances on each side. Two spiracular plates in middle of disc, each plate with B-shaped spiracular opening and 4 palmately-branched float hairs. Anal proleg a prominent transverse lobe on anterior margin of anal plate, bearing 4–5 rows of dark, decurved hooks on posterior surface. (Based on 14 specimens.)

Second instar larva: Light brown, integument transparent. Length 3.4–7.0 mm. ($\bar{x}$ = 4.7 mm.); width 0.5–1.4 mm. ($\bar{x}$ = 0.8 mm.). Resembling third instar larva in general appearance and distribution of sensory papillae and plates on segment 1, hair patches, and body tubercles. Cephalopharyngeal skeleton (Fig. 6), length 0.45–0.54 mm. ($\bar{x}$ = 0.49 mm.); with paired mouthhooks, each bearing 3 or 4 decurved accessory teeth below hook; ventral margins of mouthhooks articulating with ventral arch below, posterior margin articulating with fused hypostomal-pharyngeal sclerite behind. Ventral arch with 22–26 teeth on anterior margin, posterior border emarginate (similar to Fig. 10). Ventral cornua of fused hypostomal-pharyngeal sclerite with hyaline area or "window." Anterior spiracles located posterolaterally on segment 2; each spiracle bearing 5–6 rudimentary papillae on apical portion. Posterior spiracular disc (Fig. 2) with 4 pairs of lobes on margin; ventral pair about as long as wide, rounded apically; ventrolateral pair with broad basal portion and lanceolate dorsal projection; lateral lobes conical, pointed apically; dorsal pair low, dome-like protuberances. Two spiracular plates, each bearing 3 elongate-oval slits and 4 palmately-branched float hairs. Anal proleg a prominent lobe on anterior margin of anal plate, bearing 4–5 rows of decurved, hyaline hooks on posterior surface. (Based on 10 specimens.)

Third instar larva: Light brown, integument transparent. Length 7.1–11.5 mm. ($\bar{x}$ = 9.5 mm.); width 1.3–2.5 mm. ($\bar{x}$ = 1.8 mm.). Segment 1 bilobed anteriorly, each lobe bearing two-segmented sensory papilla and circular sensory plate; labral papilla on each side of mouth opening; no labral rami on oral lobes; postoral spine band posteroventrally, extending half-way up each side. Cephalopharyngeal skeleton (Fig. 7), length 0.65–0.81 mm. ($\bar{x}$ = 0.74 mm.); with paired mouthhooks, each with 3 or 4 slightly decurved accessory teeth beneath hook portion (Fig. 9). Ventral arch (Fig. 10) articulating with ventral margins of mouthhooks, bearing 22–28 teeth on anterior margin; posterior border irregular, emarginate. Hypostomal sclerite (HS) articulating with posterior margins of mouthhooks, in ventral view, appearing as an inverted "A"; epistomal sclerite (ES) extending over it dorsally; ligulate sclerite (LS) lying below anterior rami. Pharyngeal sclerite (PS) with dorsally-radiating pigment lines; ventral cornua (VC) with small hyaline area of "window" basally on dorsal margin. Segment 2 bearing pair of anterior spiracles, each spiracle (Fig. 4) with 5–7 papillae distally; middle third of spiracle slightly inflated. Segments 5–10 each with 2 pairs of hair patches dorsally and

dorsolaterally, each hair patch bearing 3–5 fine bristles; lateral tubercle group with 3 contiguous tubercles, middle one slightly anterior to upper and lower tubercle, each tubercle bearing 1 or 2 fine hairs; ventral transverse tubercle group of 4 tubercles, with 2 wide-set tubercles and transverse welt anterior to 4 tubercles, secondary integumentary folds prominent ventrally and laterally. Segment 11 without hair patches dorsally. Posterior spiracular disc (Fig. 1) with 2 pairs of prominent lobes; ventral pair (VL) conical, about one and one-half times as long as wide; ventrolateral pair (VIL) with broad basal portion and elongate finger-like process dorsally; lateral lobes (LL) blunt, conical protuberances; dorsolateral (DIL) and dorsal lobes (DL) low, inconspicuous protuberances. Two spiracular plates in central area of disc slightly elevated from disc surface on low stigmatic tubes (ST); each plate with three elongate slits (SS); middle slit straight; upper and lower slits angulate to arcuate. Four palmately-branched float hairs (FH) alternating with spiracular slits. Anal proleg a prominent rounded protuberance on anterior margin of anal plate, bearing 4–6 rows of decurved, hyaline hooks on its posterior surface. (Based on 13 specimens.)

Puparium: (Figs. 8, 11). Dark reddish brown, opaque. Length 4.8–6.3 mm. ($\bar{x}$ = 5.5 mm.); width 1.8–2.5 mm. ($\bar{x}$ = 2.2 mm.). Cylindrical, with ends tapering and posterior end upturned to form angle of 100–120° with longitudinal body axis. Cephalic caps projecting anteriorly; anterior spiracles conspicuous, thrust laterally at anterolateral border of dorsal cephalic cap. Hair patches not evident dorsally nor dorsolaterally; tubercle groups appearing as shagreen areas laterally and ventrally. Posterior end bearing spiracular plates apically on widely diverging stigmatic tubes. Lobes of spiracular disc shrunken, inconspicuous. Anal plate on posterior side of upturned portion; anal proleg retracted, inconspicuous. (Based on 15 specimens.)

Discussion: Protodictya hondurana larvae possess all the general features of larvae belonging to the *Tetanocerinae*, as outlined by Foote, *el al.* (1960). As with all sciomyzid larvae, *P. hondurana* has a ventral arch, an unpaired sclerite in close association with the ventral border of each mouthhook. The larvae of this species can be recognized by the emarginate condition of the posterior border of the ventral arch; the four, prominent, accessory teeth on each mouthhook; and, in the third instar, the angulate or arcuate condition of the upper and lower spiracular slits on each spiracular plate.

It should be emphasized that the second instar larva also has

three slits on each posterior spiracular plate, but that in this instar the upper and lower slits are straight. The first point deserves particular attention because of wide acceptance of the generalization that the number of openings on each spiracular plate provides a quick, reliable way of identifying the larval instar in all cyclorrhaphous Diptera. Larvae of *Atrichomelina pubera* (Sciomyzinae) uphold this generalization, having one (more or less double) opening on each plate in first instar, two slits in second instar, and three in third instar (Foote, *et al.*, 1960). However, all tetanocerine larvae that we have studied have three slits on each plate in second instar as well as in third.

The puparium of *P. hondurana*, although probably occurring more commonly in the soil than in water, has the upturned posterior end and overall shape characteristic of the floating puparia of aquatic Tetanocerinae. It can be distinguished from all other known puparia in this group by the long, diverging stigmatic tubes resulting in widely spaced spiracular plates at their ends.

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